XIV.

CONTRIBUTIONS FROM THE CRYPTOGAMIC LABORATORY OF HARVARD UNIVERSITY.

XXXIV. — ON SOME POINTS IN THE DEVELOPMENT OF ÆCIDIA.

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Very little has been published in the last twenty years regarding the development of the æcidium stage of the Uredineæ, and very little more is known than at the time when De Bary * wrote his text-book. Very recently Neumann † has given an account of the development of the æcidium, but his researches do not throw a great deal of light on the question. He is able to trace the origin of the basidia, or foot cells, as he calls them, only in a very general way, and as regards disputed points as to the formation of the peridium and the growth of the hymenium there is much to be said. Other authors have considered the question of the sexuality of the æcidium, but hardly any of them have taken it up from the developmental standpoint of the organ itself. Reference will be found to these papers in a general discussion at the end of this article.

In obtaining material for the study of the development of the æcidium it is necessary to consider several things. Not only must the material be plentiful, but the æcidium had best be a large one, and, above all, the tissues of the host of such a character as to allow of successful manipulation. For the latter purpose nothing could be better than an aquatic host, the tissues of which are usually loose, and the chlorophyll, at least in the more or less submerged portions, not so abundant as to interfere with a clear view of the hyphæ of the fungus. Nothing was found more favorable than an Æcidium on *Peltandra undulata*, which may be obtained in quantity in the neighborhood of

* Morphologie der Pilze, 1884.

† Ueber die Entwickl., der Aecidien, etc., Hedwigia, 1894, Heft 6.

Boston during the spring. Most of the work to be described was done on this form, but Æcidia on *Houstonia cærulea*, *Ranunculus septentrionalis*, *Anemone nemorosa*, and *Sambucus Canadensis*, were also studied. *Peridermium elatinum* on *Abies balsamea*, and *Rœstelia lacerata* on the fruit of *Amelanchier Canadensis*, were also examined, and some particulars regarding the later stages of the æcidium seen in the other species were confirmed.

In all the work the methods of manipulation employed were the familiar ones. Sections were made both free-hand and with the microtome. With the microtome sections the material was stained either *in toto* or on the slide; Delafield's hæmatoxylin being found most favorable for the former, while for the latter and also for the hand sections eosin, Hofmann's blue, or Mayer's acid hæmalum was used. Lactic acid was usually employed instead of potash for distending and clearing the sections, because it does not disorganize and render so exceedingly transparent the tangled masses of hyphæ as does the latter. Most of the actual work of examination and almost all of the drawings were made while the sections were still in aqueous media, for any method of mounting soon renders the specimens so transparent that it is impossible to see the details. For final mounting, glycerine was usually preferred to balsam, although for the study of the nuclei specimens stained with hæmatoxylin and mounted in the latter were found the best. As is usual in the studying of structures of this sort, where certain differentiated portions must be disengaged from tangled masses of filaments, it was found that a tolerably thick section, properly dissected and macerated, was often more instructive than even a complete series of thinner ones.

Æcidium on Peltandra.

This form, which is the æcidium of *Uromyces Caladii*, being the one which was most thoroughly worked up, will be taken up first, to be followed by a discussion of the other forms named. The first material used for this examination was collected by Professor Thaxter, who kindly placed it at my disposal; quantities of the same æcidium have been collected by myself several times since, and the material killed in both picric and chromic acids. In selecting the portions of the plant for sectioning, petioles were usually taken, as they were easier to cut and also contained less chlorophyll than the leaves. By taking pieces of considerable length and cutting longitudinal sections the young æcidia could be traced with ease.

For the earliest stages, pieces of tissue in which with a hand lens nothing but the spermogonia could be detected were taken. In sections of these, the youngest stages of what De Bary called "primordia" were seen, which consist of a large number of branching hyphæ, which are massed together and finally become compacted into an irregular sized ball. Even the youngest conditions may be distinguished from developing spermogonia, both by the fact that they are embedded more deeply in the leaf, and also because the hyphæ are more loosely arranged than in a spermogonium of equal size. After this massing together of the hyphæ to form the primordium has kept on for a certain time, changes are seen to take place. The hyphæ already septate become very much more so, and the small cells so formed begin to enlarge very much. The result is that a large part of the primordium now consists of a pseudo-parenchyma of cells of very irregular size and shape, and with walls of very variable thickness. Finally, the whole primordium changes to this pseudo-parenchyma with the exception of a weft of tightly woven hyphæ around the periphery, which merge at the base into a mass of somewhat more loosely compacted threads. A careful search was made in these young stages to determine if anything in the nature of a trichogyne could be found, but in all of the sections examined nothing to which the function of a trichogyne could be ascribed was seen. Occasional hyphæ were seen protruding out of the stomata, but they did not connect with any of the primordia, and showed no evidence of any specialization.

During the formation of the pseudo-parenchyma, the young æcidium increases very much in size, and consequently displaces the cells of the host plant. The primordium, starting in a large intercellular cavity, fills it, and then the hyphæ, pushing out, soon surround the neighboring cells, and often cut them off from their fellows. Such isolated cells are usually completely broken down by the hyphæ, and apparently absorbed. In this case practically no distortion accompanies the growth of the hyphæ or æcidia.

Earlier than the formation of the pseudo-parenchyma no sign is seen of the hymenium, nor can the hyphæ which are to form it be distinguished. At about this stage, however, there arises at the base of the primordium a definitely differentiated hypha, which may in respect to its further development be called the fertile or sporogenic hypha. It is to be distinguished from the ordinary sterile hyphæ which surround it by its highly granular and somewhat more refractive contents. It absorbs aniline stains slowly, but to a great amount,

finally becoming much more deeply colored than the surrounding threads. It is not, however, very easy to demonstrate, and many sections must be examined before obtaining the fortunate ones which will show it.

At first the fertile hypha presents no very characteristic form, but as time goes on it becomes twisted sometimes almost spirally (Fig. 1). Although usually simple in the beginning, later it may fork, or even branch several times. This fertile hypha may be traced down in among the mass of threads at the base of the primordium, and there is nothing to indicate that it originates from any specialized organ, but simply from the undifferentiated mycelium. The subsequent development of it which leads to the formation of the hymenium is subject to some variation. In the smaller æcidia the fertile hypha simply begins to bud out at the tip into short projections which are young basidia (Fig. 2), but in the larger æcidia it may branch so that the hymenium may arise from several points (Fig. 3). In this species the contents of the fertile hypha very soon pass into the buds of the young hymenium, leaving it empty and quite indistinguishable from the surrounding hyphæ. Following the development of one of the smaller Æcidia, it is seen that the buds rapidly increase in number and assume a more definite position. The larger older ones are usually in the centre of the cluster, and the young buds are formed around the periphery (Fig. 4). The young basidia are cut off from the central mass as fast as they are formed, and after enlarging somewhat show other cross septa, which are the first indications of what may be called the spore mother cells. To make room for the developing hymenium, the pseudo-parenchyma usually splits at this juncture. A rift is formed in the centre of the primordium, and, the cells around it collapsing, there is left a large cavity into which the young basidia push up (Fig. 2). As the basidia increase, they finally compress the pseudo-parenchyma, until in the mature æcidium it is seen only as a narrow covering outside of the peridium, made up of the collapsed and almost disorganized cells which formerly filled the whole primordium.

The development of the hymenium in the larger æcidia is essentially the same, except that in place of a single compacted mass of basidia they arise over a somewhat larger area or from several distinct points (Fig. 3). Soon, however, the basidia form a solid mass, and, although there is a certain amount of intercalary formation, most of the growth of new basidia takes place around the periphery of the hymenium.

The septation of the basidia which started in the older ones is continued by the younger ones near the periphery, and the next definite change that is to be noted is the beginning of the peridium. The formation of the peridium commences by the differentiation of the terminal cells cut off from the older basidia. Their walls become definitely thicker and their contents very vacuolate, presenting quite a distinct difference from the spore mother cells below (Fig. 3). As the other young spore chains push up, their terminal cells also become similarly altered and the formation of the peridium progresses rapidly from the centre outwards. The peridial cells so formed increase more rapidly in size than the spores below, and owing to this and the interpolation of new basidia, which grow up from the base, their connection with the chains of cells from which they originated is often lost. Sometimes, however, this connection is retained quite clearly even when the æcidium is well along in its development, due perhaps to the fact that in such cases the young basidia have grown up more nearly simultaneously than usual and that there has been no intercalary formation of basidia. At times the enlargement of the peridial cells is more rapid than need be to cover the hymenium as it enlarges, in which cases they may be pushed out of place so as to give the appearance of a double layer of cells.

This metamorphosis of the terminal cells continues to the very margin of the hymenium, and there the same modification affects the whole peripheral row of spore chains, so that the æcidium is now completely incased in a covering of modified spores which may be called the peridium. This last point is shown better in other æcidia than the one now under discussion, and will be referred to later. Nothing was seen that would lead one to suppose that the peridium originated around the periphery and grows up until it meets in the centre, nor did it appear that it is derived in any way from the pseudo-parenchyma layer, for the line of demarcation between this and the peridium is always apparent (Fig. 3).

Concerning the formation of the spores there is not much that is new to be said. They are cut off basipetally from the basidia or foot cells, and the cells thus formed are being constantly pushed up by the formation of new ones below. The upper row forms, as has already been described, the peridium; from the others the spores are produced. In these cells may be seen a double nucleus, or rather two nuclei almost always in close proximity to each other (Fig. 5, *a*). These have already been described by Rosen,* and also by Dangeard, but as

* Cohn's Beitrage, VI.

my own observations as to the fate of these nuclei do not entirely correspond with Rosen's view, there remains something to be said about them. The cells which are first cut off from the basidia are not the spores themselves, for from their proximal end is always cut off a small usually wedge-shaped cell (Fig. 6, *a*, *b*) the interstitial cell of De Bary. The larger upper cell becomes the spore, the small lower one eventually disappearing.

In the basidia there are always two and often more nuclei. When a spore mother cell is about to be cut off one of these migrates to the tip and there divides, a septum is soon formed below it, and the spore mother cell is formed. Rosen states that when the interstitial cell is about to be cut off, each of these twin nuclei divides, and from the four daughter nuclei so formed two migrate to the lower end of the cell, where they are cut off, and the other two remain in the spore proper. In my own observations in by far the majority of cases the nuclei separated without dividing, and were separated as single nuclei, one in the spore and one in the interstitial cell (Fig. 6, *a*). The nucleus in the spore always divided at least once, — in a considerable number of cases, indeed, three nuclei were seen in the ripe spores (Fig. 5, *b*, *c*), — while the nucleus in the interstitial cell sometimes divided, but quite as often remained single, as long as the interstitial cell persisted. As the spore ripens, the wall thickens and becomes rough, the interstitial cell disappears, and the spore may be said to be mature. The double nucleus remains quite distinct in the spore to the oldest stages.

In speaking of the double nuclei in the spore it should be mentioned that they are found in all of the other parts of the æcidia, in the hyphæ, the pseudo-parenchyma, and the peridium. This ubiquity tends to deprive them of so great a significance as some authors have placed upon them.

It is not necessary to follow the development of the æcidium any further, the final rupturing of the peridium, etc. having been often described in other forms.

Æcidium on Houstonia cærulea.

Most of the material used for the examination of this species was collected by Professor Thaxter, who kindly allowed me free use of it. A small amount collected by myself at Sharon, Mass., was killed in picric acid, and was valuable for some of the younger stages. This æcidium is found both on the leaves and corolla of its host. The

leaves, owing to their comparatively loose structure, and to the fact that the chlorophyll was mainly disorganized by the fungus, proved the best for use.

In the mature æcidium nothing of note is to be observed which differs from the æcidium already described. The layers outside of the hymenium are better developed and the peridial cells and spores smaller than in the æcidium on Peltandra. The whole æcidium is more compact. The intercalary cells are very prominent and in them, perhaps on account of their large size the double nuclei are usually easily seen.

The fertile hypha appears at about the same stage as noted before. When it is traced back it is seen to merge into the rest of the mycelium, and at first can only be told by its more granular and refractive contents. Perhaps the best case observed was seen in Figure 7, where at the base of a young primordium is seen a very much twisted highly granular hypha which has already sent out a branch from which the hymenium will develop, as in Figure 8. In the somewhat older æcidia the young basidia may be seen to radiate very distinctly from a common centre, which marks the position presumably of the end of the fertile hypha (Fig. 9).

The subsequent development of the spores and peridium accords well with that already described in the previous case, with the exception of the fact that the pseudo-parenchyma does not split as in the æcidium on Peltandra, but is gradually pushed aside as the hymenium develops.

Æcidium on Ranunculus septentrionalis.

On the lower sides of the leaves and on the petioles of Ranunculus this species of æcidium may be found occurring in clusters, with the older æcidia in the centre and the younger around them. A considerable quantity of the material was collected by myself in the vicinity of Cambridge in the spring of 1894.

The mature æcidia present no great peculiarities, with the exception of a very considerable variability in the size of the peridial cells. Ordinarily they are large, much larger than the spores, but occasionally specimens are found with very much smaller cells. In such cases, it is quite easy to trace their connection with the spore chains below: they differ but little from the spores in size, but have the characteristic walls of peridial cells. It is possible that this condition may be explained by a delay in the formation of the peridium in such cases. The hymenium having attained its full size, there was not the same

necessity for the rapid growth of the peridium to cover it. Interstitial cells are present, and do not show anything unusual. The usual double nuclei were easily demonstrated in all the various parts of the æcidium.

This æcidium proved more favorable than some to demonstrate the connection of the basidia with the fertile hyphæ. In one fortunate macerated preparation a somewhat tortuous hypha was seen, from which branches arose that terminated directly in the basidia (Fig. 11). The character of the leaf was not favorable for the study of the younger stages, as the compacted condition of the tissue and the presence of much chlorophyll obscured the young primordia. Nevertheless, several interesting stages were seen that are worthy of note since they help to substantiate the observations made on the other æcidia. In Figure 10 a section of a young æcidium is shown where the fertile hypha has pushed its way into the already fully developed pseudo-parenchyma. From the fertile hypha, in which many nuclei could be made out, there have arisen the first buds from which eventually the basidia and spores will be formed. Unfortunately this otherwise excellent section was marred by the fact that the hypha was cut off only a short distance below the place where it had begun to bud out. Its connection with the hypha below, as indicated by the dotted lines, was only inferred by the similarity of their contents and general appearance. At this early stage no septa could be seen that cut off the buds from the parent hypha. Other stages of a similar sort, some younger and others older, were found, but none showed as clearly as the one just described. A very much younger condition, where the fertile hypha is but a simple thread with a rounded end and rich in granular contents, was perhaps the earliest condition observed. In some of the larger æcidia, which however never approached the size often attained by the æcidium on Peltandra, ther were apparently more than one point of origin for the basidia.

Æcidium on Anemone.

This form, which is *Æcidium punctatum* Pers., is in many respects unfavorable for examination, but, as it was apparent that it presented some variation from the type already described, some work was undertaken on it. The æcidia do not occur in clusters, as in some other cases, but are more or less scattered over the under side of the leaf; but they have a certain advantage over other æcidia in that the spermogonia being so very superficial there is never any danger of confusing the young stages of these two organs.

The basidia are comparatively short, and the layer below them, which may be called the sub-hymenial layer, is much more closely compacted than in any of the forms previously described in this paper. It is also noticeable that the base of the hymenium, which in other cases, at least in the younger stages, is often somewhat rounded, is here practically flat, since the basidia almost all terminate on the same level. The primordium progresses in its development without much variation from the general rule, except that the amount of pseudo-parenchymatic tissue is relatively smaller, and the surrounding weft of hyphæ relatively larger than in the three æcidia already described. It was evident from the appearance of the young hymenium, in which the basidia develop much more nearly simultaneously than in the cases already noted, that there was some variation in the development of this form from the types previously examined.

Below the young basidia in the sub-hymenial layer there could be distinguished fertile hyphæ, from which the basidia are budded out, and sterile hyphæ that wound in among them (Fig. 12). The former could be separated from the latter on account of their power of staining deeply. This layer of sporogenous hyphæ which underlies the pseudo-parenchyma gives rise to the basidia more nearly at the same time than they arise, for instance, in *Æcidium Caladii*, although even here it is apparent that the younger basidia are the ones nearer the periphery of the hymenium. The fertile hyphæ arise from the branching of hyphæ that make their way up from below, and apparently the sporogenous layer may arise from more than one of such hyphæ. This course of development much more nearly corresponds to that given by Neumann * than any of the others do, but is not exactly as he describes it in the æcidia he investigated.

It was in this species especially that hyphæ were seen protruding through the stoma, but examination failed to show any connection of such hyphæ with the primordia, and it was probably due more to the very great crowding of the mycelium in the leaf than to any other cause. The subsequent development of the spores and peridium failed to reveal any noteworthy peculiarities. This æcidium is especially interesting as showing a variation from others in the matter of its development, but a discussion of this point will be reserved until a few words have been said about some other æcidia which afforded interesting facts, especially regarding the formation of the peridium.

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* *Loc. cit.*.

Aecidium on Sambucus.

In this æcidium there is a considerable amount of distortion of the tissues of the host, but at present only the æcidium itself will be considered. It did not afford a very good chance for studying the younger stages, but, as nearly as could be made out the development corresponds more nearly to that of the æcidium on Ranunculus than to any other.

The peridium begins in the usual way from the metamorphosis of the terminal cells in the older spore chains, and spreads over the top of the hymenium, as already described. The fact that the side walls of the peridium correspond to the outer row of spore chains is excellently shown in this species. The peridial cells, which become smaller and thinner walled as they approach the base of the hymenium, are seen finally to merge into a foot cell which exactly resembles the other basidia. In the youngest peridial cells even the interstitial cells were observed, although De Bary in his text-book says that they are not present in the peridium (Fig. 13). Very soon, of course, owing to the enlarging of the peridial cells and to the thickening of their walls, the interstitial cells disappear sooner than they do between the spores.

Passing to the Æcidium known as *Peridermium elatinum*, we find an interesting variation in the formation of the primordium. What may be properly called the primordium in this case is but poorly developed, consisting of simply a mass of loosely arranged pseudo-parenchyma of rather large cells, and with none, or practically none, of the hyphal weft about them. It is not improbable that this form might prove a very excellent one for studying the young stages of the hymenium, and it is greatly to be regretted that the material at hand was too advanced for that purpose. The formation of the peridium, however, showed admirably. In Figure 14 a young æcidium is shown, in which two peridial cells have just begun their differentiation from the spore chains. The mature æcidium, aside from the necessary reduction of the mass of collapsed pseudo-parenchyma outside of the peridium, showed no great peculiarities.

The last æcidium to be considered is Rœstelia. It was hoped that, owing to the long period of formation that the Rœsteliæ undergo before they emerge through the tissues of their hosts, it might be coupled with some longer preparatory growth of the æcidium itself. Such, however, did not prove to be the case, for in all of the species examined, although the origin of the Rœstelia was very deep in the tissues of the host, and consequently it was a long time in

breaking through, the spores and peridium began to form as early as in the other æcidia. The subsequent development was simply a multiplication of the spores and peridial cells. In the species chiefly examined, *Rœstelia lacerata* on *Amelanchier Canadensis*, there were however some facts made out that should be mentioned.

The mass of pseudo-parenchyma in the primordium is elongated vertically, and appears still to keep on forming, while the hymenium is developing, until it almost reaches the surface of the tissue in which it lies. Although excellent young material was obtained, it was impossible, owing to the very compact and obscure nature of the primordium and the very small size of the hyphæ, to make anything out of the youngest stages even by all the various methods tried. The young basidia are very narrow, and those which form the peridium swell abruptly into the peridial cells, which at first, though large, are very thin-walled. The intercalary production of basidia is more marked here than in any æcidium previously examined, and owing to this the connection of the peridial cells with the spore chains is rapidly lost. The cells of the peridium, which are at first about the normal shape, lengthen very much, and become of the elongate almost rhomboidal shape found in the mature æcidium.

General Discussion of the Æcidium Stage.

In comparing the results of the foregoing observations with the accounts of the development of the æcidium already published certain differences of considerable importance will be noticed. As regards the formation of a primordium with a mass of pseudo-parenchymatic cells in the centre, there appears to be a general unanimity of opinion, although Neumann* figures the formation of the hymenium at a much earlier stage than seems to be the case in the æcidia described here or in those mentioned in previous accounts. In Plate XVI. Fig. 3 of his paper he shows very definite indications of a hymenium before the appearance of the compact pseudo-parenchyma. The same is true of his figure of the æcidium on *Ficaria ranunculoides*, but if one may judge from the drawing of the form on *Euphorbia Cyparissias*, the condition is more nearly as I have seen it myself, where there is a definite pseudo-parenchyma before the formation of the young basidia. Concerning the formation of the sporogenous hyphæ, there seems to be but little better knowledge in the pub-

* *Loc. cit.*

lished accounts than there was at the time De Bary wrote his text-book. All that De Bary says is, that after the formation of the primordium with its pseudo parenchyma, "the hymenium now makes its appearance at the base of the æcidium," etc.* He also leaves in doubt the question of the manner in which the hymenium increases in area, whether it is by the peripheral or intercalary formation of new basidia. Plowright † throws no light on either question, leaving them just as De Bary has. There is really nothing which deals with the question further, until we come to Neumann's paper already mentioned. Even here the matter of the origin of the basidia is passed over somewhat vaguely, being referred to as being cut off from the hyphæ. In the question of the enlargement of the hymenial surface, it will be seen that his conclusion and the one put forward in this paper do not entirely coincide. He expresses the opinion that all of the basidia arise practically simultaneously, and that one cannot speak of any after-growth of new ones. This is certainly not the condition found in the æcidium of Peltandra, or of forms like it, although in the æcidium on Anemone something more nearly approaching it is seen. The opinion of De Bary that the hymenium usually starts from a comparatively small centre is borne out by my own observations. The opinion expressed here, which seems to have basis in the facts observed, is that the formation of new basidia, while mainly peripheral, is also to some extent intercalary, and that in most æcidia they are not formed simultaneously.

As regards the origin of the basidia Neumann adds but little, and there have been practically no suggestions in this direction except a very brief account by Massee ‡ of the occurrence of an oögonium which after fertilization by an antheridium, after the manner of the Peronosporeæ, grew out into the basidia. It is unnecessary to do more than refer to this publication, and to add that, so far as the observations recorded here go, nothing of such a nature was discovered. There are, however, certain definite fertile hyphæ which rise from the mycelium and push their way into the primordium. It has also been seen that these hyphæ are often twisted, even spirally bent, suggesting possibly the "Woronin's hyphæ" seen in the development of certain Pyrenomycetes. From these hyphæ are given off buds or branches

* De Bary, Comp. Morph. of the Fungi and Mycetogoa, Garnsey and Balfour's trans., page 274.

† British Uredineæ and Ustilagineæ, 1889, p. 22.

‡ Annals of Botany, 1889.

which give rise to the basidia. At this point there is apparently some difference in the development of different species, and even in the æcidia of the same species. In the æcidia on Peltandra and Houstonia, at least among the smaller ones, the basidia arise with but little branching on the part of the fertile hypha, while in the form described on Ranunculus the fertile hypha seems to branch to some extent, and in the æcidium on Amemone it forms apparently an extended growth before giving rise to the hymenium. It is probable that in some cases, particularly in the larger æcidia, more than one fertile hypha takes part in the formation of the hymenium.

In the formation of the spores, there is first formed what may be called the spore mother cell, from which by division is formed the spore itself and the small interstitial cell, in the manner previously described. Plowright * speaks of the spores as being formed *in* a mother cell, and that by subsequent growth and thickening of the walls the spore and the mother cell fuse together. Such, however, can hardly be considered the state of affairs, for the intercalary cell is plainly cut off in the manner described by Rosen and also given in this paper.

Regarding the peridium, the view advanced here is probably more different from the generally accepted idea than any other particular mentioned in this paper. Almost everywhere one finds the statement that the peridium originates along the sides and "arches over" the hymenium. De Bary has said that the cells of the peridium do not possess intercalary cells, but this is hardly the case in the æcidium herein described on Sambucus, although in other cases the thickening of the wall might begin before it was time for the intercalary cell to be formed, in which case its production might be interrupted. It might be objected that the union of the terminal cells with the peripheral spore chains to form the peridium is hard to account for, but when one considers the condition of affairs in the young æcidium it is not so difficult to understand. The walls of the young peridial cells are very delicate, and, being under a relatively considerable pressure, are literally forced together. It is true that in their subsequent development the peridial cells on the side increase mainly in length, while the peridial cells on the top of the æcidium increase in all directions; but that is hardly an unsurmountable objection. It may be that it is the pressure under which the cells of the peridium are formed which induces the excessive thickening of the wall.

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* *Loc. cit.*, p. 22.

It has been the view of some writers that the peridium is the result of a development from a circle of paraphyses, and the condition of the æcidium of Phragmidium is cited in support of this view. But, as De Bary * has said, the paraphysal envelope of this æcidium is not well understood, and no light has been thrown on this matter since he wrote regarding it. Whatever may be the condition in this æcidium, however, it is safe to say that the peridium of the ordinary æcidium is the result of a metamorphosis of the outer layer of spores.

As to what interpretation is to be placed upon the æcidium, and what place it occupies in the life history of the Uredineæ, so much has been said, and so little comparatively is known, that a re-discussion cannot bring out much that is new. What has been described in this paper, although perhaps not of the most positive nature, certainly rather supports than contradicts the view held by De Bary. In the æcidia here investigated, it would seem that the æcidium is not to be regarded at the present time as the result of a sexual process, but that it has a definite spore-bearing hypha, possibly corresponding to the archicarp.

Some of the more recent writers in text-books have entirely disregarded De Bary's view, and speak of the Uredineæ as forms of fungi with three chlamydosporic stages, in some cases comparing the chains of æcidiospores and their interstitial cells with the chlamydospores found in Chlamydomucor. This seems to carry it to somewhat of an extreme, for one certainly does not associate with chlamydosporic conditions such relatively complicated sporocarps as are found in the Uredineæ.

Vuillemin † has recently published an account of the æcidiospores, in which he maintains to have found the equivalent of a sexual stage in the union of the double nuclei found in these spores. The question of the sexuality of such a process, should it occur, can hardly be discussed here, for the idea itself naturally suggests its own objections, particularly in the light of the ubiquity of the double nuclei throughout the Uredineæ. It is interesting to note in this connection a fact already recorded, that triple nuclei have been not infrequently seen.

To sum the whole question up, it seems to the writer that the view expressed on this question by De Bary, where he likens the æcidium to the sporocarp, has more basis in fact than any other theory, but that at the present time there is no sexuality in the process of the forma-

* *Loc. cit.*, p. 246.

† Comptes Rendus, 1893, Vol. CXVI. p. 1464.

tion of this sporocarp. Hartig* has said that it is probable that the æcidium is the result of a preceding sexual act, and is therefore a true sporocarp, like the perithecium and apothecium of the Ascomycetes. This is stating the case strongly, but even if the æcidium is not the result of a sexual act, it does not preclude the comparison with the sporocarp, for it has been abundantly shown that the sexuality in the formation of the latter is often much reduced among many fungi, the Ascomycetes in particular.

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* Diseases of Trees, Trans. Somerville and Ward, p. 153.

CRYPTOGAMIC LABORATORY, HARVARD UNIVERSITY,
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EXPLANATION OF PLATE.

Æcidium of Uromyces Caladii on Peltandra.

1. Section of primordium showing fertile hypha. × 320.
2. Older stage, where the fertile hypha has begun to bud. × 320.
3. Young stage of a large æcidium showing several points of origin of hymenium. The peridium has begun to form. × 320. *a.* Showing the formation of the peridium at a somewhat later stage. × 320.
4. More advanced stage of same. The pseudo-parenchyma has ruptured. × 320.
5. *a.* Single ripe spore showing double nucleus. *b.* Spore with three nuclei. × 1250.
6. Young spore just cut off from the basidium showing nuclei. *b.* Spore; older, but not yet mature. × 1250.

Æcidium on Houstonia cærulea.

7. Section of primordium with fertile hypha. × 320.
8. Older stage, showing connection of fertile hypha with young basidia. Not quite median although showing the fertile hypha. × 320.
9. Section of young æcidium, showing a somewhat older hymenium. × 320.

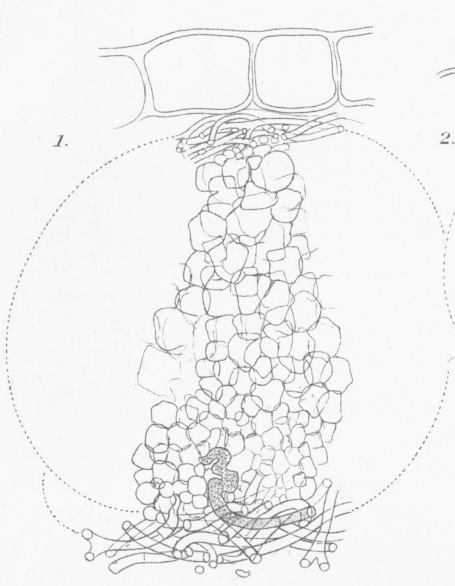
Æcidium on Ranunculus.

10. Section of primordium with fertile hypha already budding. × 320.
11. Section of an almost mature æcidium, in which the connection of the fertile hypha with some of the basidia is plainly shown. × 320.

12. Young basidia from æcidium on Anemone (*Æcidium punctatum*). The sterile hyphæ, the contents of which are not so granular, show among the fertile ones. × 560.
13. Margin of a section of æcidium on Sambucus, showing origin of the peridium. × 560.
14. Young æcidium of *Peridermium elatinum*. × 320.

All the drawings were made with the aid of an Abbé camera and reduced about one third in reproducing. Figures 3, 3 *a*, 4, 5, 6, 7, 9, and 14 were drawn from microtome sections, the rest from hand sections. All were treated with lactic acid, and stained before drawing.

H.M. Richards - Æcidia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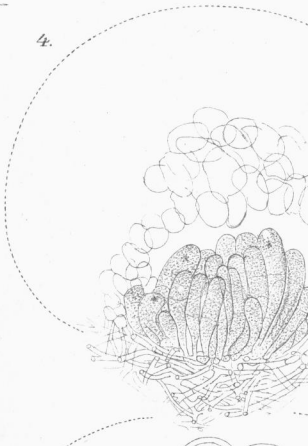
2.


3.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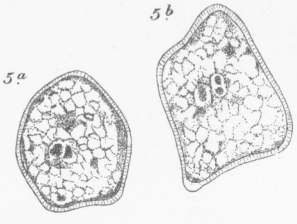
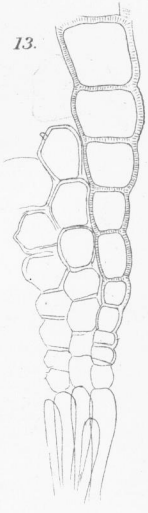

5a 5b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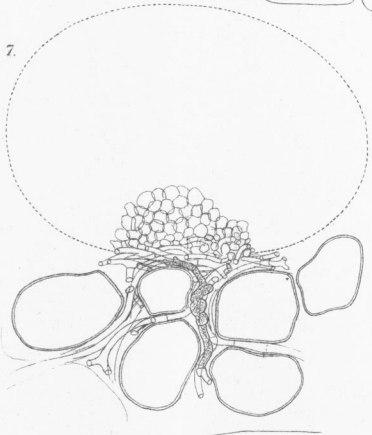
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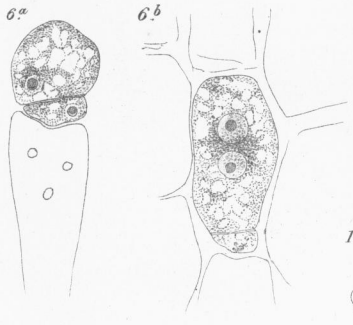
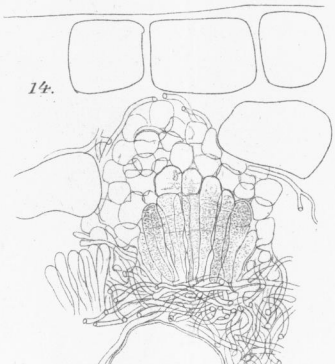

6a 6b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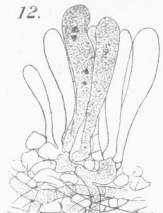
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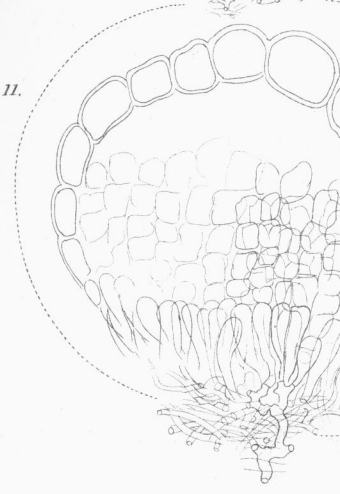
3a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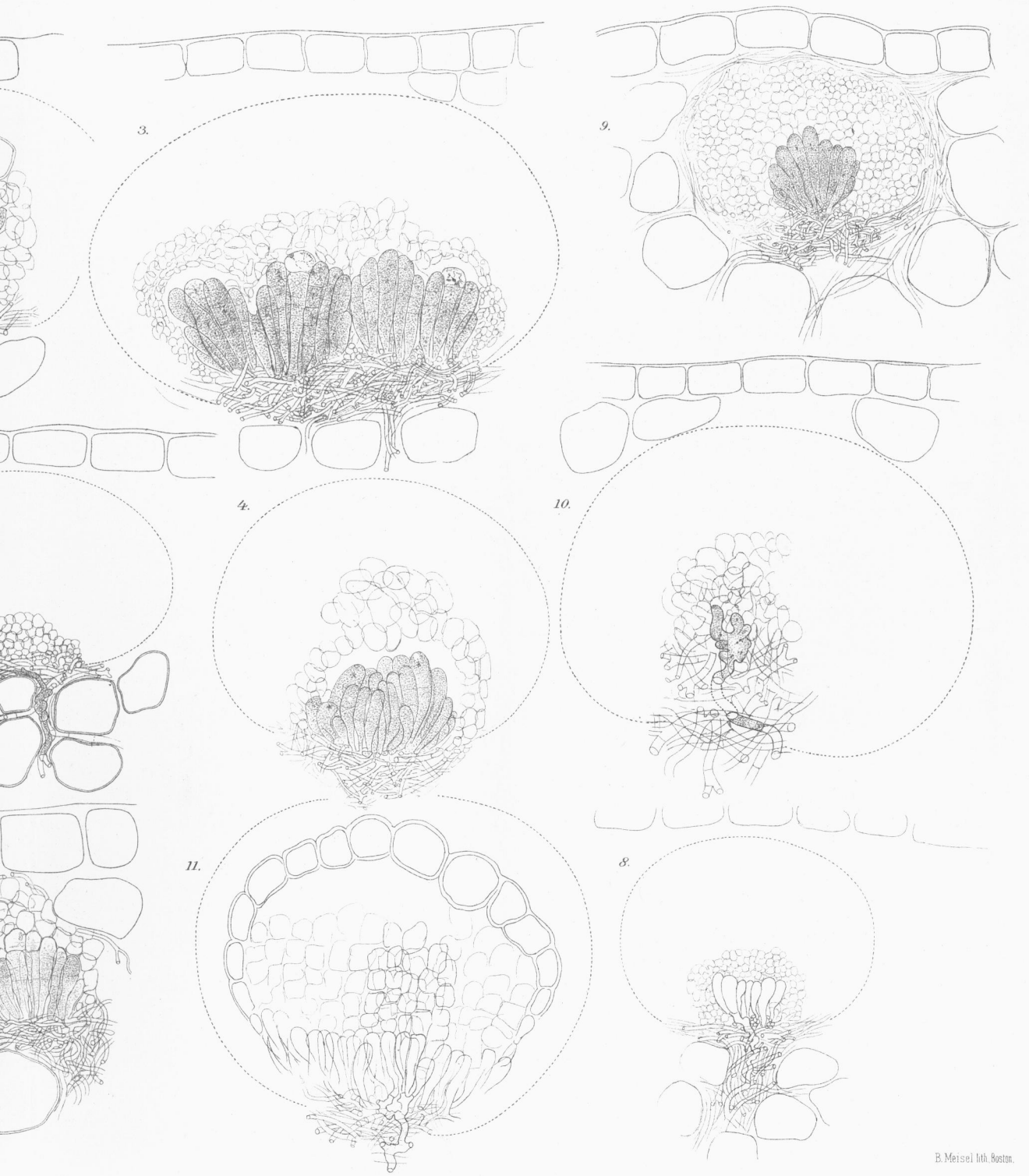
H.M.R. del.



B. Meisel lith. Boston.